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ORIGINAL ARTICLE

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Determinants of the re-occupation and size of Grey Heron *Ardea cinerea* breeding colonies in northern Poland

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Abstract Birds select habitats on the basis of structural characteristics, food and nest-site availability or other features that affect survival and reproduction. This study investigates factors influencing colony re-occupation, the number of nests in 2013 and changes in the numbers of nest between 2004 and 2013 in re-occupied colonies of Grey Herons *Ardea cinerea* in northern Poland. The effects of following features around every colony were analysed: area of hydrographic and habitat features, habitat patchiness and microscale features. Among 28 colonies occupied in 2004, 43 % were re-occupied in 2013. Logistic regression models revealed that models with greater area of the sea coastline zone and lower area of the water body shoreline zone and also small number of pastures determined the best colony re-occupation. Only models with an area of water bodies and a number of pastures were significant, suggesting the important influence of other non-habitat factors on colony re-occupation. Ordinary least square (OLS) regression analysis revealed that in re-occupied colonies the number of nests in 2013 was higher in heronries with greater area of sea coastline zone, smaller number of forest patches and shorter distance to the nearest road. OLS regression analysis revealed that the number of nests increased between 2004 and 2013 in the colonies with greater areas covered by forests, greater number of water bodies, shorter distance to the rivers and longer distance to the sea. Our study revealed the importance of wetland habitat features to colony re-occupation, its size and changes in size.

Keywords Colony re-occupation · Colony size · Grey Heron · Hydrographic features · Habitat features

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Introduction

Identification of key habitats is necessary to understand why species attain a particular pattern of distribution and abundance across the landscape (Wiens et al. 1986). Birds select habitats on the basis of structural characteristics (Drent and Daan 1980; Cody 1985; Martin 1987; Newton 1998). Habitat selection is especially important for colonial breeders affecting their colony size and reproductive success (Werschkul et al. 1976; McCrimmon 1978; Beaver et al. 1980; Furness and Birkhead 1984; Marion 1989; Boisteau and Marion 2007; Kazantzidis et al. 2013). Thus, the knowledge of how different habitats and other factors affect their occurrence is crucial to an understanding of their breeding ecology. The role of the environment in the distribution of the population depends on the biology of the species (Atauri and Lucio 2001), especially in terms of foraging specialization (specialists, opportunists) and movement abilities. Colonial breeding also provides opportunities for mate selection, social stimulation to start and synchronize the nesting cycle, and increased choice of mate selection (Kushlan et al. 2005). An important factor determining the colony size may be competition for places to nest e.g. in the Northern Gannet *Morus bassanus* (Nelson 1966), or food availability in herons, cormorants, alcids, gannets and gulls (Werschkul et al. 1976; McCrimmon 1978; Beaver et al. 1980; Furness and Birkhead 1984). Colonial breeders such as herons serve as a good model species to study the influence of landscape features on the distribution of population, because the location of their breeding colonies is not random (Gibbs et al. 1987; Gibbs and Kinkel 1997; Boisteau and Marion 2006; Kelly et al.

2008). Herons prefer areas where the foraging grounds provide potentially large availability of food (Ward and Zahavi 1973; Kushlan 1976, 1978; Marion 1988; Gibbs 1991; Gibbs and Kinkel 1997). Most colonies are located in the centre of wetland complexes (Gibbs 1991; Gibbs and Kinkel 1997). Diet composition depends mainly on local and seasonal availability of certain types of food (Cramp 1998).

The Grey Heron *Ardea cinerea*, is a colonially breeding waterbird. Its diet consists mainly of fish but also of other prey, such as small mammals, amphibians, reptiles and aquatic insects (Milstein et al. 1970; Draulans et al. 1987; Jakubas and Mioduszewska 2005; Jakubas and Manikowska 2011). Considering the food preferences of the Grey Heron, hydrographic network is an important landscape element which affects the location of breeding colonies (Boisteau and Marion 2006). However, given the variability of the Grey Heron diet (Cramp 1998; Jakubas and Mioduszewska 2005; Jakubas and Manikowska 2011), other habitats such as meadows/pastures may also serve as important feeding areas. It has been reported that the presence of very large rivers, waterways and floodplains or swamps/inland marshes within a 25 km radius around the colony determined the location and size of the Grey Heron colonies in France (Boisteau 2002). The location of heron colonies centrally to the wetland complexes may reduce the range of foraging trips between the colony and foraging grounds (Gibbs and Kinkel 1997). In the case of the Great Blue Heron *Ardea herodias*, a positive correlation between the size of the colony and the availability of wetlands has been reported (English 1978; Gibbs et al. 1987; Gibbs 1991). The human impact on habitats can have a negative effect on the distribution of the population (Hansen et al. 1993). It has been reported that the presence of humans negatively affects the selection of nesting sites of the Great Blue Heron (Bjorklund 1975; Werschkul et al. 1976; Henny and Kurts 1978; Gibbs et al. 1987; Watts and Bradshaw 1994). The negative influence of human disturbance on breeding has also been reported for Grey Herons (Kitowski and Krawczyk 2005; Jakubas and Manikowska-Ślepowrońska 2013). Nevertheless, many waterbirds tolerate regular human activity close the colony (Nisbet 2000). The Grey Heron regularly breeds in close proximity to human residences (Kushlan and Hafner 2000).

The main aim of this study was to identify factors (hydrographic/habitat area and others) influencing the re-occupation of a colony site in successive years of Grey Heron breeding colonies in northern Poland. Large heronries in Poland occur mainly in the studied region (Tomiałojć and Stawarczyk 2003) characterized by postglacial landscape with high number of lakes and large areas covered by forest (Kondracki 2002). Studies on factors affecting re-occupation of the breeding colonies have never been conducted before on the Grey Heron and have rarely been conducted on other *Ciconiiformes* (e.g. Wyman 2012). The second aim of the study was to investigate factors influencing the number of nests in the occupied colonies and the temporal changes in the number of occupied nests. Specifically, we expected that:

1. Colonies situated closer to water bodies/rivers and canals/sea (due to energy limitation of foraging flights) would be occupied more frequently and would be characterized by an increase in the number of nests compared to those situated further from such habitats.
2. Colonies situated in the forest (i.e. less conspicuous for predators, less exposed to human disturbance) would be more re-occupied than those situated in small forest patches or on lake islands.
3. Colonies situated closer to buildings or roads would be less re-occupied (due to the negative influence of human disturbance) than those situated further from human settlements.
4. A large number of aquatic habitat patches would be positively correlated with the colony size as they may indicate many different foraging areas.
5. A low number of forest patches would be positively correlated with the colony size as a larger forest patch may serve as buffer zone against human disturbances.

Methods

Study area

The study was performed in the northern part of Poland (part of the Middle European Plain). The study area includes a circular area within a radius of 170 km around the Vistula River Mouth (51,108 km^2 excluding sea; Fig. 1) and it comprises parts of the following subprovinces (according to the physico-geographical regionalization of Poland; Kondracki 2002): South Baltic and East Baltic Coast, South Baltic and East Baltic Lake District. This area includes the coast of the Baltic Sea with peninsulas (Hel Peninsula and Vistula Split) and bays and lagoons (Gdańsk Gulf, Vistula Lagoon). The landscape consists of coastal zone comprised of: dunes, coastal cliffs, reedbeds, large coastal lakes, river mouths and salt marshes. The East Baltic Coast comprises Żuławy Wiślane, the lowland in the alluvial delta area of the Vistula river, in large part reclaimed artificially by dykes, pumps, channels and extensive drainage systems. It is a deforested, agricultural plain that covers 1000 km^2 (Fac-Beneda 2000). The inland area with lake districts is characterized by post-glacial landscape with moraine hills (up to 309 m) and outwash plain (Kondracki 2002). In the studied area, non-irrigated arable land, forests and lakes made up 54, 33 and 2 % of the area, respectively.

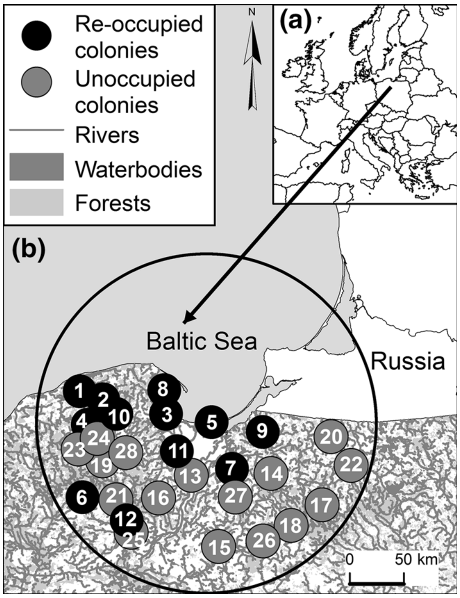

Fig. 1 Localization of 28 studied breeding colonies of Grey Herons in northern Poland (*black circles*—colonies re-occupied in 2013, *grey circles*—unoccupied in 2013, occupied in the past; *large circle* shows the area within a radius of 170 km around the Vistula Mouth [location of the study area in Europe (**a**) and in N Poland (**b**)]. Names and numbers of colonies—see Tables 1 and 2

Table 1 Number of nests in breeding colonies of Grey Herons occupied in 2004 and 2013

No.	Colony	No. of nests		Change rate between 2004 and 2013 (%)*
		2004	2013	
1	Będziechowo	46	13	−126
2	**Chocielewko**	**57**	55	−4
3	Gdańsk-Oliwa	23	29	23
4	Jawory	14	46	119
5	**Kąty Rybackie**	**734**	326	−81
6	**Kiełpinek**	**79**	50	−46
7	**Kiersity**	**294**	125	−86
8	**Mosty**	**340**	194	−56
9	**Płoskinia**	**60**	23	−96
10	Skrzeszewo	21	44	74
11	Turze	Lack of data	26	
12	Wełpin	25	89	127

Large colonies (with ≥50 nests in 2004) are bolded. No.—numbers of colonies refer to the numbers in Fig. 1

*- after $\ln(N_{2014}/N_{2003}) * 100$ transformation

Fieldwork

The study was conducted in 28 breeding colonies of Grey Herons in northern Poland in 2013 (Fig. 1; Tables 1, 2). We visited the majority of colonies which were occupied in 1999–2009 according to Żółkoś et al. (2010). In 2013, 12 colonies were re-occupied (Table 1) and 16 were unoccupied (Table 2). In the case of the unoccupied, abandoned colonies, the last occupancy year was estimated based on information from foresters and local residents. All the colonies were visited during the breeding season in 2013, between the last ten days of April and mid-June during the chick-rearing period of Grey Herons. In each colony all nests were counted twice during the same control by the same two people.

Data analysis

To identify factors influencing re-occupation and size of the Grey Heron breeding colonies, the effects of following landscape features within a radius of 20 km around the colony (corresponding to the average distance flight foraging trips for this species; Marion 1989) were analysed:

1. hydrographic and habitat features:

(a) hydrographic features (Table 3) based on water databases concerning the status and quality of Europe's rivers, lakes, groundwater bodies and transitional, coastal and marine waters, and the quantity of Europe's water resources (http://www.eea.europa.eu/data-and-maps/data/waterbase-rivers-9, European Environment Agency, The European Topic Centre on Inland, Coastal and Marine waters. Version 13, 2013). We considered deeper parts of the rivers, lakes and sea are usually inaccessible for foraging herons. It has been reported that hydrographic features (potential foraging areas) serve as important landscape factors affecting the location of breeding colonies of the Grey Heron (Marion 1989; Boisteau and Marion 2006).

(b) habitat features (Table 3) based on Corine Land Cover (http://www.eea.europa.eu/, EEA Copenhagen, 2012). This model contains information on land cover derived from Landsat 7 satellite images; we used CLC2006 model—the year 2006 update of the basic CLC1990 model. We combined all types of forest. As urban zone we considered the following habitat types: airports, construction sites, continuous urban fabric, dumpsites, industrial or commercial units, mineral extract sites, port areas, road and rail networks and sport and leisure facilities; the area of inland marshes is indicative of the presence of potential foraging areas; an area covered by urban zone is indicative of areas exposed to human disturbance.

2. habitat patchiness based on Corine Land Cover (CLC2006) model (Table 3). We analysed habitat heterogeneity (number of habitats and linear features and total patchiness) A large number of aquatic habitat patches may indicate many different foraging areas; a low number of forest patches may indicate wide buffer zones against human disturbances around the colonies.
3. microscale features based on maps from Geoportal (http://mapy.geoportal.gov.pl):

Table 2 Breeding colonies of Grey Herons unoccupied in 2013

No.	Colony	No. of nests (year)	Year/period when the colony was abandoned
13	Benowo	**69** (2004)	2008
14	Bogaczewo	10 (1980)	before 1991
15	Czekanowo	42 (2003)	2010/2011
16	Kałębnica	46 (2004)	2008
17	Kośno	38 (1999)	1999–2006
18	Lake Mielno	**61** (1999)	1999–2006
19	Lake Somińskie	9 (2004)	2004–2013
20	Lusiny	**65** (1999)	2005–2012
21	Lutom	**70** (2004)	2009
22	Łężany	20 (1999)	1999–2006
23	Masłowice	**67** (2004)	2013
24	Pomysk Mały	12 (2006)	after 2006
25	Czapliniec Koźliny	40 (2004)	2006
26	Czapliniec Werski	45 (1999)	1999–2006
27	Czerwica	**69** (2006)	after 2006
28	Wierzysko	26 (2004)	~2010

Large colonies (≥50 nests in 2004) are bolded. No.—numbers of colonies refer to the numbers in Fig. 1

(a) distance from the centre of the colony to the nearest water body, river or sea; this is an important variable affecting the time and energy budget of parent birds commuting to/from foraging grounds: the smaller the distance, the lower energy expenditures;
(b) distance from the centre of the colony to the nearest building and road: the greater the distance from a colony to buildings and roads, the lower the risk of human disturbance; this factor can have a strong negative effect on the colony size and re-occupation, but susceptibility to human disturbance also varies among species (Nisbet 2000; Kazantzidis et al. 2013);
(c) colony location [on the island/in the big forest patches (> 60 ha)/in the small forest patches (≤ 60 ha)]; colonies located in the bigger forest patches are less conspicuous for predators and less exposed to human disturbance.

All the spatial variables were derived from models and maps using ArcGIS software, version 9.3 (ESRI, Redlands, California, USA).

Statistical analysis

To investigate which landscape features determined colony re-occupation, number of nests in 2013 and changes in their number between 2004 and 2013, we analysed three non-collinear sets of variables, i.e. hydrographic features and habitat area (Pearson correlation coefficients, $r < |0.44|$), habitat patchiness (Pearson correlation coefficients, $r < |0.41|$) and microscale features (Pearson correlation coefficients, $r < |0.42|$). Considering the relatively small sample size, separate analyses for three datasets were performed and only models with maximum two predictors were constructed.

To analyse factors determining re-occupation of colonies, logistic regression analysis was used. Additionally, to study whether the size of the colony affected its re-occupation, the proportion of unoccupied and re-occupied sites among large (i.e. with ≥50 nests in 2004) and small heronries was compared using χ^2 test. To investigate whether colony location (on the island/in the big or small forest patches) affected colony re-occupation, χ^2 test with Yates' correction was used. To analyse factors affecting the size of colonies re-occupied in 2013 and changes in the size (in %) of re-occupied colonies between 2004 and 2013 (9 years), ordinary least square (OLS) regression analysis was used. Data pertaining to changes in the number of nests between 2004 and 2013 were analysed after $\ln(N_{2013}/N_{2004})$ transformation. Due to the lack of historical data from one colony, only 11 colonies were included in the analysis of changes in colony size.

To select the best model determining colony re-occupation, number of nests in 2013 and changes in their number between 2004 and 2013, we used Akaike's information criterion for small sample size (AIC_c) (Burnham and Anderson 2002; Mazerolle 2006; Hegyi and Garamszegi 2011). To compare the relative performance of the models, the difference (ΔAIC_c) between the AIC value of the best model and AIC value for each of the other models and Akaike's weights (Burnham and Anderson 2002) were calculated. Akaike's weights (w) can be interpreted as the probability that a model is the best model for observed data given the candidate set of models. The sum of all Akaike's weights is 1 (Mazerolle 2006). When $\Delta AIC_c < 2$, the given model was suggested to be within the range of plausible models to best fit the observed data (Burnham and Anderson 2002). Significance of OLS regression models was checked using Wald statistics. As the AIC_c provides evidence for selection of the best model from the set, but does not permit evaluation of discriminatory performance, we used the receiver operating characteristic to assess the classification accuracy of the best models (Pearce and Ferrier 2000). Our criteria for the predictive capability was based on area under the receiver operating characteristic function (AUC) where good models had a value of ≥0.7 and poor models had a value of < 0.7 (Hosmer et al. 2013). We also assessed the effectiveness of the best logistic regression models by: (1) examining the proportion of occupied and unoccupied colonies that were classified correctly using all cases in the analysis (self-test); (2) cross-validation (each case is classified by the functions derived from all cases other than that case); (3) due to the unequal sample sizes of unoccupied and occupied colonies, a chance-corrected procedure (Cohen's kappa statistic) was used to determine if the classification was better than random (Titus et al. 1984; Berg et al. 2004).

All statistical analysis were performed in R software (R Development Core Team 2007) with MuMin (Bartoń 2013), aod (Lesnoff and Lancelot 2012), and pROC (Robin et al. 2011) packages, IBM SPSS Statistics 21

(IBMSPSS, Chicago, Illinois, USA) and STATISTICA 10 (Statsoft Inc. 2011). The accepted significance level was $P < 0.05$.

Results

Factors affecting the colony re-occupation

Among 28 colonies occupied in 2004, 43 % were re-occupied in 2013. The area covered by sea coastline zone and water body shoreline zones were the best predictors of colony occupation in the set of hydrographic and habitat variables (Table 3). However, only the model ranked as the third according to ΔAIC_c, with the area of water body shoreline zones had relatively high AUC score (0.82) suggesting bigger utility for determining colony re-occupation (Table 4). Re-occupied colonies were characterized by low area of water body shoreline zones (Table 4). This model correctly classified 78.6 % of the studied colonies. The result of the cross-validation test produced the same results. Chance-corrected procedure showed that classification was 56.0 % (Cohen's kappa = 0.56, SE = 0.19, $P = 0.002$) better than chance. There were no unoccupied colonies with the coastline within 20 km radius around the heronry. The first model with sea coastal zone and water body shoreline zones and the second with sea coastal zone correctly classified 78.6 % (Cohen's kappa = 0.56, SE = 0.19, $P = 0.002$) and 75.0 % (Cohen's kappa = 0.55, SE = 0.21, $P = 0.02$) of the studied colonies, respectively. The predictive capabilities of both models were relatively low (AUC $\leq$ 0.71; Table 4). Re-occupied colonies were characterized by lower area of water body shoreline zone and larger area of sea coastal zone (Table 4).

Among habitat patchiness variables, two models containing number of pastures and inland marshes determined the best colony re-occupation (Table 4). Re-occupied colonies were characterized by low number of pastures (Table 4). This model classified correctly 75.0 % of the studied colonies. The result of the cross-validation test produced the same result. Chance-corrected procedure showed that classification was 52 % (kappa = 0.52, SE = 0.19, $P = 0.006$) better than chance. In the second model, Re-occupied colonies were characterized by low number of inland marshes The predictive capabilities of both models were relatively low (AUC > 0.86; Table 4).

Among the microscale variables, further distance to the nearest building and closer distance to the nearest water body were the best predictors of colony re-occupation. However, predictive capabilities of this model, as well as others based on microscale variables were low (AUC < 0.7; Table 4). The best model classified correctly 64.3 % of the studied colonies. Chance-corrected procedure showed that classification was only 52.0 % (kappa = 0.52, SE = 0.20, $P = 0.10$) better than chance.

The proportion of unoccupied and re-occupied sites among large (≥50 nests) and small heronries was similar (1:0.5 and 1:0.6, respectively; χ^2 test, $\chi^2_{26} = 0.77$, $P = 0.38$). The proportion of unoccupied and re-occupied colonies was similar among colonies located in small and large forest patches (1:0.4 and 1:1.4, respectively; χ^2 test with Yates' correction, $\chi^2_1 = 0.81$ $\chi^2_1 = 0.81$, $P = 0.37$).

Factors affecting the colony size

The number of nests in 12 colonies occupied in 2013 ranged from 13 to 326. The area of sea coastline zone was the best predictor of the number of nests in 2013 in the set of hydrographic and habitat variables (Table 3). Larger colonies were characterized by greater areas of sea coastline zone (Table 5).

Table 3 Codes for hydrographic and habitat features, habitat patchiness and microscale variables

Variable code	Variable	Comments
Hydrographic and habitat features, habitat patchiness		
Sea	Sea coastline zone	Area: coastline length × 2 m shallow water zone potentially accessible for foraging herons Patchiness: each occurrence in the buffer was considered as independent patch
WatBod	Water bodies shoreline zone	Area: linear length × 2 m considering 1 m width zone on both sides potentially accessible for foraging herons;
RivCan	Rivers and canals bank zone	Patchiness: each occurrence in the buffer was considered as independent patch
For	Forests	Area: area covered by particular type of habitat
Past	Pastures	Patchiness: number of patches of particular type of habitat
InlMar	Inland marshes	
NonIrri	Non-irrigated arable land	
Urb	Urban zone	
TotPatch	Total patchiness	Patchiness: number of all considered patches
Microscale variables		
DisRiv	Distance to the nearest river/canal	Distance from the centre of the colony to the nearest river
DisWatBod	Distance to the nearest water body	Distance from the centre of the colony to the nearest water body
DisRoad	Distance to the nearest road	Distance from the centre of the colony to the nearest road
DisUrb	Distance to the nearest building	Distance from the centre of the colony to the nearest building
DisSea	Distance to the sea	Distance from the centre of the colony to the Baltic Sea

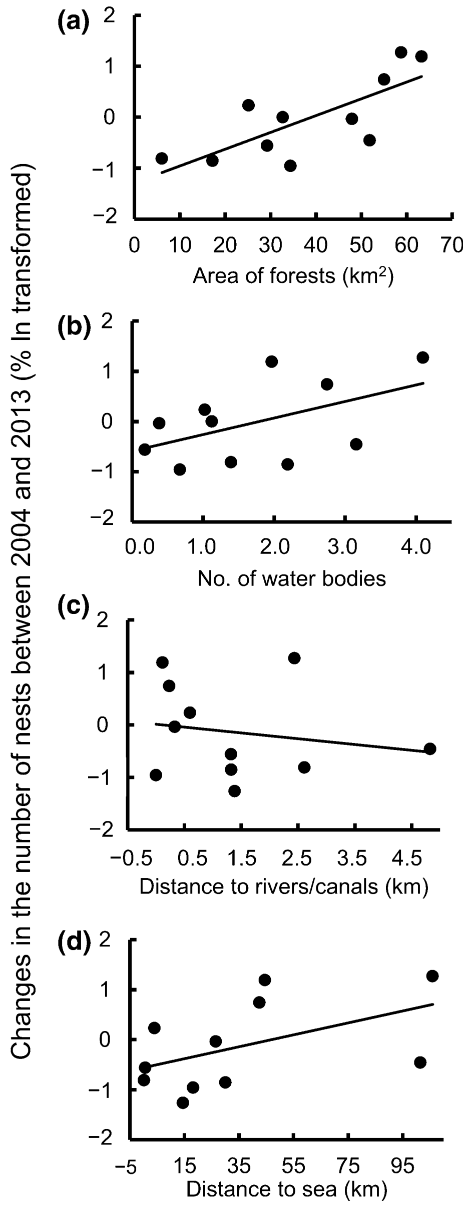

Fig. 2 Relationship between changes in number of the Grey Heron nests between 2004 and 2013 (ln transformed) and: (**a**) area covered by forests (km^2), (**b**) number of water bodies, (**c**) distance to the nearest rivers/canals and (d) distance to the sea within 20 km radius around the heronry ($N = 11$)

The number of forest patches was the best predictor of colony size in the set of patchiness variables. The number of nests in colonies increased with decreasing number of forest patches (Table 5).

Among the microscale variables, two models were significant (Wald test, $P < 0.001$; Table 5). However, parameters in both models were insignificant: in the first model, the colony size increased with the distance to the nearest road (Table 5) and in the second with the distance the water bodies (Table 5). Despite insignificant parameter estimates, determination coefficients were not very low ($R^2 = 0.48$ and 0.37 for the first and second function, respectively).

Factors affecting changes in size of re-occupied colonies

In the re-occupied colonies, the number of nests changed between 2004 and 2013. Difference between 2004 and 2013 was negative in 64 %, and positive in 36 % of the colonies. There was a 59 % decrease in the number of nests in all colonies combined. The negative difference was observed both in small colonies (< 50 nests; −126 % in Będziechowo and −96 % in Płoskinia) as well as in larger ones (≥50 nests; −86 % in Kiersity and −81 % in Kąty Rybackie), while the positive difference was observed mainly in small colonies Wełpin (+127 %), Jawory (+119 %) and Skrzeszewo (+74 %) (Table 1). There was no large colony with a recorded increase in the number of nests.

The area covered by forests was the best predictor of changes in the number of nests in re-occupied colonies. Increase in the colony size was recorded in areas with higher area of forests (Fig. 2, Table 5).

For the patchiness set, the number of water bodies was the best predictor of changes in the number of nests in re-occupied colonies (Table 5). The number of nest increased in areas with greater number of water bodies (Fig. 2, Table 5).

Among the microscale variables, distance to the nearest river/canals and distance to the sea were the best predictors of changes in the colony size (Table 5). The number of nests increased in colonies situated further to the sea and closer to the river/canals (Fig. 2, Table 5).

Discussion

Our study revealed that the Grey Heron colonies in northern Poland were more frequently re-occupied in sites with lower numbers of pastures, smaller area of water body shoreline zone and greater area of sea coastline zone. A positive influence of the sea coastline zone on both re-occupation and numbers of nests was expected as coastline, especially its shallow parts, is frequently used by Grey Herons as foraging area because its anatomical structure restricts foraging mainly to shallow water zones (Marion 1989; Cramp 1998; Boisteau and Marion 2007). In our study, all the colonies situated within a 20 km radius of the coastline, were re-occupied. Herons from coastal colonies may have foraged both in marine and inland freshwater foraging areas. Foraging in the marine environment enables them to start breeding earlier in the spring, when most inland water bodies are still covered with ice (Jakubas 2011). Preference for lower area of water body shoreline zone is surprising. It may be explained by the specificity of water bodies in northern Poland. Majority of them are represented by postglacial lakes, among

Table 4 Rank of the best logistic regression models for factors determining re-occupation, of the Grey Heron colonies in the north Poland using hydrographic and habitat features, habitat patchiness and microscale variables (codes in Table 3) based on Akaike's Information Criterion corrected for small sample size (AIC_c)

Model	AIC	ΔAIC_c	Akaike's weights (*w*)	AUC
Hydrographic and habitat features				
Int + Sea − WatBod	31.5	0.00	0.32	0.69
Int + Sea	32.7	1.25	0.17	**0.71**
Int − WatBod	32.8	1.35	0.17	**0.82**
Int – NonIrri − WatBod	33.4	1.86	0.13	0.59
Int + Sea + Urb	33.4	1.88	0.13	**0.76**
Habitat patchiness				
Int − Past	27.9	0.00	0.36	**0.87**
Int − InlMar − Past	29.5	1.58	0.16	**0.88**
Microscale variables				
Int − DisUrb + DisWatBod	37.6	0.00	0.36	0.50
Int + DisWatBod	38.6	1.01	0.22	0.66
Int − DisUrb	39.2	1.62	0.16	0.69

Akaike's weights (w) is calculated from the full set of models. The predictive capability of functions based on area under the receiver operating characteristic function (AUC); good models (AUC ≥ 0.7) bolded
Int intercept

Table 5 Rank of the best OLS regression models for factors determining size of the colony and change in size of re-occupied colonies of the Grey Heron colonies in the north Poland using hydrographic and habitat features, habitat patchiness and microscale variables (codes in Table 3) based on Akaike's Information Criterion corrected for small sample size (AIC_c)

Model	AIC	ΔAIC_c	Akaike's weights (*w*)	Wald test *P*
Colony size				
Hydrographic and habitat feature				
Int + Sea	132.3	0.00	0.42	< 0.001
Int + Sea − Urb	134.0	1.64	0.18	< 0.001
Habitat patchiness				
Int − For	132.5	0.00	0.56	< 0.001
Microscale variables				
Int + DisRoad	135.8	0.00	0.37	< 0.001
Int + DisWatBod	136.4	0.58	0.28	< 0.001
Changes in size of re-occupied colonies				
Hydrographic and habitat features				
Int + For	28.6	0.00	0.30	0.005
Int + For − Past	29.6	0.93	0.19	< 0.001
Habitat patchiness				
Int + WatBod	31.0	0.00	0.33	0.03
Int + RivCan	31.6	0.63	0.24	0.051
Int + NonIrri	32.2	1.16	0.18	0.07
Microscale variables				
Int − DisRiv + DisSea	33.3	0.27	0.24	0.02
Int − DisWatBod	33.3	0.27	0.24	0.14
Int + DisSea	33.8	0.78	0.16	0.19
Int − DisUrb	34.6	1.61	0.11	0.30
Int − DisUrb − DisWatBod	34.9	1.91	0.09	0.05

Akaike's weights (*w*) is calculated from the full set of models. Model significance estimated by Wald test; significant models bolded
Int intercept

which ribbon lakes that are characterized by large surface areas and very steep edges/banks. In the Pomeranian Lake District, there are many small oligotrophic lakes (Bajkiewicz-Grabowska 2009), sparse in food attractive to Grey Herons. Thus, only some types of water bodies are characterized by shoreline zone accessible as foraging area for herons. Generally low predictive capabilities of models determining colony re-occupation suggests that other non-habitat factors (e.g. demographic processes, predation, siblicide, population density) may better determine colony re-occupation.

In our study, larger colonies were located in areas with smaller number of forest patches. The greater number of forest patches around the colonies is often connected with high number of small forest patches. Positive relationship between the area of forests and changes in number of nests in re-occupied colonies suggests that Grey Herons prefer compact forest patches creating wide buffer zones against human disturbance. Moreover, large area of forests often indicates a smaller area of habitats managed by humans (agriculture, urban zones) which may be exposed to habitat destruction (e.g.

drainage). Negative influence of pasture patches on colony re-occupation and pasture area on changes in nest in re-occupied colonies suggest that Grey Herons avoid this potentially suitable foraging habitat as it is often considerably transformed by human activities (e.g. by draining).

Changes in the number of nests in re-occupied colonies were positively related to greater area of forests, greater number of water bodies, shorter distance to the nearest rivers/canals and longer distance to the seashore. Both water bodies and rivers/canals are optimal foraging areas to herons. Those results were expected because these habitats serve as important foraging areas for Grey Herons as well as other herons (Boisteau and Marion 2006; Kelly et al. 2008; Jakubas and Manikowska 2011; Kazantzidis et al. 2013). The studied species forages on freshwater prey (Owen 1960; Milstein et al. 1970; Draulans et al. 1987; Lekuona 2002; Jakubas and Mioduszewska 2005; Jakubas and Manikowska 2011), especially during the breeding season (Fasola et al. 1993). All those factors have also been recognized as important determinants of Grey Heron colony location (Boisteau and Marion 2007). Also, other species of herons prefer large areas covered by wetlands or linear banks (Gibbs 1991; Farinha and Leitão 1996; Gibbs and Kinkel 1997). Furthermore, in France, high density both of small and large rivers suggesting uniform distribution of feeding territories positively affected colony size (Boisteau and Marion 2007). The large rivers in Poland are regularly stocked by the Polish Angling Association and Inland Fisheries Institute, so they may serve as attractive foraging ground to the Grey Herons. Increase in number of nests in re-occupied colonies was higher in colonies situated further from the seacoast. It seems to contradict positive influence of the area of sea coastal zone on colony re-occupation and colony size. However, it may just indicate different demographic processes in coastal colonies usually larger than inland ones.

Among significant microscale effects, longer distance to the nearest road positively affected colony size, while shorter distance to the nearest building negatively affected re-occupation. Close proximity to roads and buildings is considered as index of human disturbance. Studies from Greece indicated that human proximity (expressed by the distance of a colony to the nearest road and village) negatively affected the nest abundance in Grey Heron colonies (Kazantzidis et al. 2013). On the other hand, Grey Herons are known for breeding in close proximity to human residences (43 % of 69 colonies in north Poland are located <500 m from buildings; Żółkoś et al. 2010), even in ornamental parks in city centres (e.g. in Amsterdam, London, Nilrjik, Oléron; Cramp 1998; Kushlan and Hafner 2000). However, breeding in such neighbourhood may have negative impact on reproductive success and colony size (Jakubas and Manikowska-Ślepowrońska 2013). Nesting in close proximity to human activity not always negatively affects waterbirds. It might provide suitable foraging opportunities in human-altered portions of the landscape, such as rice fields (the most significant man-made foraging habitat for breeding herons in the Mediterranean, due to the variety, density and size of prey organisms, as well as the suitability of water depth and substrate; Fasola et al.1993; Fasola and Ruiz 1996; Maeda 2001; Czech and Parsons 2002; Kazantzidis and Goutner 2008; Longoni 2010), fish ponds (Kushlan et al. 2005; Kloskowski 2011; Manikowska-Ślepowrońska et al. in preparation). In our study, the colony at Jawory with 119 % increase in number of nests between 2004 and 2013 is situated in close proximity (110 m) to the fish farm ponds.

Interpreting re-occupation and changes in the colony size in re-occupied colonies, various natural processes should be considered (e.g. environmental and climatic change and species interactions; Skagen et al. 2001). In addition, human-induced environmental changes (e.g. habitat transformation or modification) and wildlife management (persecution, protection) are directly or indirectly related to population trends, often becoming an issue of conservation concern (e.g. McCulloch et al. 1992; Tucker and Heath 1994; Marion 1997; Newton 1998; Donald et al. 2001; Stenseth et al. 2002; Gaston et al. 2003; Duhem et al. 2008; Kloskowski 2011; Jakubas and Manikowska-Ślepowrońska 2013; Manikowska-Ślepowrońska et al. in preparation). Over recent decades, environmental changes have been observed in the agricultural landscape of Poland. After the accession of Poland to the European Union in 2004, some areas were eliminated from agricultural use, triggering secondary succession which led to the decline of patches of semi-natural meadow, moor and marshy communities (Bomanowska and Kiedrzyński 2011). In the case of the absence of colony-site disturbances, colonies may grow until they reach the carrying capacity of the environment (Kushlan et al. 2005), so the number of nests/pairs of breeding birds could reach a maximum number of individuals which are able to forage in a specific area. The colony size of the Grey Heron is regulated by feeding territoriality: in France, the radius of the foraging grounds around the colony is highly correlated with the number of breeders (Marion 1979). Desertion of 57 % studied colonies and general decline in the size of re-occupied colonies (−59 %) observed in this study, although recorded in the limited area, is consistent with a decrease in the breeding population of Grey Herons recently observed in Poland (Kitowski and Krawczyk 2005; Chylarecki and Jawińska 2007; Chodkiewicz et al. unpublished data). The reason for this trend is unknown. In some areas the disappearance of colonies, or a drastic decrease in the number of nests was attributed to human disturbance (disturbance by military jets, shooting foraging birds at fish ponds and the destruction of nests, regular pedestrian traffic and the noise of machines in close proximity to the colony; Kitowski and Krawczyk 2005; Jakubas and Manikowska-Ślepowrońska 2013).

In conclusion, our study revealed the importance of aquatic habitats to colony size and changes in size. This result supports the use of the Grey Heron as an indicator species for environmental monitoring in freshwater ecosystems (Marchant et al. 2004). Our results suggest that colony re-occupation is probably determined better by other non-habitat factors as demographic processes, predation, siblicide or population density. Although we did not specifically measure population change, our results suggest a decline in the local breeding population. When investigating changes in the colony size, it is important to consider several factors, such as environmental and climatic changes, human disturbance and species interaction. There is no available data regarding such changes in the studied area. However, some processes in aquatic environments which may have affected the Grey Heron population size have been recognized [e.g. a decrease in the number and diversity of fish in rivers in central Poland and in the main lake districts (Masuria, Pomerania, Greater Poland) caused mainly by eutrophication (Kruk 2004; Mickiewicz 2012; R. Chróst—unpubl. data)]. We are aware that our limited dataset (based on limited number of colonies and landscape variables) is insufficient to recognise factors affecting colony re-occupation and size. The data presented here can, however, be treated as a pilot study contributing to the planning of a broad-scaled investigation covering a wider area and further variables. Nevertheless, our study has filled an evident gap in knowledge about the relationship between Grey Heron colonies re-occupation and size, and landscape features.

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